Field, Lab and Modelling Study of Microscale Copepod Distributions

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LONG-TERM GOAL

To understand the *in situ* microscale (cm's) and fine-scale (m's) relationships between copepods and their phytoplanktonic food source, and to explore how copepods in the upper ocean are regulated by, and forage within their phytoplanktonic food.

OBJECTIVES

The objectives of the research are to understand how copepod ingestion and swimming behavior change over short (<2 hour) time scales, under a suite of different food and acclimation conditions. New techniques to determine the gut content of individual copepods are being developed to relate individual behavior to individual feeding success. Models will be used to test hypotheses of copepod foraging strategies in patchy environments. The models will be parameterized with laboratory data, and forced with data gathered from the LUMIS and FishTV deployments (Jaffe and Franks, parent grant).

APPROACH

Acartia clausi, one of the dominant coastal calanoid copepods in temperate waters, was chosen as the key organism for the research. It is a major food source for larval fish, it eats diatoms and dinoflagellates, and has only minimal effects of previous feeding history on current feeding, making it an excellent animal for laboratory manipulation. Animals were caught locally and then conditioned under different feeding and temperature regimes before being placed in the experimental aquaria for the video experiments. Animals were videotaped at high magnification for up to two hours as they fed and swam within the small aquaria. During the course of the video experiment, copepods were taken every ten minutes from replicate vessels containing animals that were similarly acclimatized as the animals in the video aquaria. These copepods were frozen in liquid nitrogen for later measurement of gut fluorescence. Within the aquaria, small vertical patches of phytoplankton were created by slow layering of waters of slightly different densities and phytoplankton concentrations.

The video was digitized into a computer for analysis of the swimming motions of the copepods: swimming speed, direction, and types of swimming behaviors were examined in relation to the length of time in the experimental chamber, acclimation regime, and gut content. These relationships were then used to parameterize one- and two-dimensional (2D) individual based simulation models of copepods swimming through theoretical and field-measured distributions of food. The 2D model can use the fluorescence data collected from the LUMIS device as the food distribution, if fluorescence is assumed to be a good indicator of amount of available phytoplankton.

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To examine natural gut content levels, individual variability in gut contents, and to investigate whether copepod populations were mixing vertically over short time scales, copepods were collected regularly from the field and immediately frozen in liquid nitrogen for later fluorometric analysis of gut contents. Coincident casts of a CTD/fluorometer/transmissometer were made at the site.

WORK COMPLETED

Twelve video experiments of copepod swimming behavior, with eight including a gut fluorescence component, and two additional gut fluorescence *versus* turbulence level experiments, have been conducted so far. Four additional experiments examining gut contents alone, without video or turbulence, have been conducted. Pre-experimental feeding acclimation has ranged from starvation for 24 hours before the experiment, to fully saturating food levels for 24 hours. Experiments have also been run before dusk, at dusk, and after dusk, in order to examine any effects that endogenous rhythms or light levels may have on the swimming and feeding behavior of the copepods. The digitized data from 2 of the experiments have been analyzed for swimming behavior, digitizing has begun on an additional experiment, and the gut fluorescence from 5 of the experiments have now been analyzed.

The 1D individual-based model (IBM) has been used to conduct a detailed theoretical study of the advantages a copepod might gain, in theoretically created and high-resolution field-sampled phytoplankton environments, using the very simple foraging strategy of a biased random walk. This work is in the final stages of preparation for submission for publication. Additionally, the 2D IBM of copepods foraging through a patchy food environment is complete, and has been used to look at the effects of foraging success of copepods within homogeneous versus non-homogeneous thin layers of phytoplankton. With the incorporation of a detailed metabolic model based on the work of Caparroy and Carlotti (1996), this work will also be ready for submission for publication to the journal Marine Models Online in the very near future.

Field collections of copepods were again made during July and August 1998, once per week, to complement the samples taken during summer 1997. Additional monthly samples were collected in April and May for comparison purposes. Samples were taken from two depths: above and below the seasonal thermocline. Gut fluorescence of the target species was determined for 10 of the dates from 1998 and compared with predictions of gut fluorescence based on a simple analytical model forced by data from CTD/fluorometer taken at each sample site. Some of these samples have been analyzed separately for individual gut content levels; however, this work continues.

RESULTS

Results from the video laboratory experiments examining behavior *versus* time since the addition of a pulse of food to the experimental aquaria have shown an increase in the time spent "jumping" *versus* a control tank with no additional food added. Because the three behaviors which these copepods exhibit – a slow cruise-type swimming, a rapid upward jump, and no movement or sinking – are mutually exclusive, a decrease in the time spent sinking was found to complement the increase in time spent jumping for the copepods in the treatment group of this experiment. Gut content analysis has shown that these copepods fill their guts within 30 minutes of addition of food, and then show a slow decrease in gut content during the rest of the experiment. Additionally, turbulence appears to decrease the rate at which these copepods fill their guts; however, individual variability appears to be large, and needs further analysis to assess its effects on the video experiment results.

The 1D model results indicate that a simple biased random walk – a decrease in step length with an increase in food concentration, but no directionality to swimming – can lead to aggregations of copepods within local food maxima. When high-resolution field-sampled phytoplankton profiles were smoothed, the theoretical behavior did little to increase the foraging success of the copepods. This emphasizes the importance of sampling the environment at the appropriate resolution when looking at the foraging motions of small organisms. The 2D model results indicated that, similar to the 1D model, copepods could gain a foraging advantage by using a correlated biased random walk. The results of this model also indicated that if thin horizontal phytoplankton layers are actually comprised of smaller 3D blobs of phytoplankton (as indicated by some of the results from the LUMIS and OSST developed on the parent grant), copepod grazing would be much lower than predicted from homogeneous layer models.

From the field sampling program, we found that copepods at the surface usually had higher (up to a factor of 2) gut fluorescence levels than deeper-caught copepods. This was contrary to our predictions, as the lower temperatures and higher fluorescence at depth should have led to higher gut fluorescence there. Copepods fill their guts within 30 minutes and empty their guts on the order of several hours, and can swim the 20-30 m distance between the surface and the deeper sampled area in under 30 minutes. Because copepod gut fluorescence levels were never the same between depth and surface samples, it appears that surface and deeper copepod populations are not mixing on short (< a few hours) time scales.

IMPACT/APPLICATION

The laboratory results of a rapid increase in gut contents followed by a change in jump behavior after encountering a patch, suggest that other relationships between feeding and swimming behavior should exist. Through our theoretical 1D and 2D modeling work, we see evidence that a successful strategy for foraging in patch structures similar to those we have measured in the environment require the copepod to respond quickly to the presence of a patch in both feeding and swimming behavior (within minutes) in order to stay within the patch. This is consistent with the laboratory data. Additionally, our modeling work strongly suggests that we must sample the environment on the same scale as copepod responses in order to properly gage the grazing impact and foraging success of a copepod. Finally, the field data showing a gut content difference in animals separated by only 10 m vertically indicates that these animals must be mixing at rates slower than 60 minutes (the time it takes to fill and empty their guts), otherwise they would all have a similar amount of gut fluorescence. This indicates that they must be maintaining their vertical position behaviorally. These findings are a significant first step towards the understanding of how a herbivorous copepod deals with its patchy environment, and the daily spatial ambit of its activities.

RELATED PROJECTS

1 – The gut fluorescence and modelling work have been used to stimulate novel sampling programs with the LUMIS fluorescence imaging system developed in the parent grant (Jaffe and Franks).

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